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Analysis of Hellenic Durum Wheat (*Triticum turgidum* L. var. *durum*) Germplasm Using Gliadin and High-molecular-weight Glutenin Subunit Loci

I.N. XYNIAS[1]*, N.A. KOZUB[2,3] and I.A. SOZINOV[2]

[1]Plant Production Department, School of Agricultural Technology, T. E. I. of Kalamata, Antikalamos, 24 100 Kalamata, Hellas
[2]Institute of Plant Protection UAAS, Vasilkovska St., 33, Kyiv 03022, Ukraine
[3]SI Institute of Food Biotechnology and Genomics NASU, Osipovskogo St., 2a, Kyiv 04123, Ukraine

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Allele composition of 12 Hellenic commercial cultivars and 17 local populations of durum wheat was evaluated at the gliadin *(Gli-A1, Gli-B1, Gli-A2, Gli-B2)* and high-molecular-weight glutenin subunit loci *(Glu-A1, Glu-B1)*. Acid polyacrylamide gel electrophoresis (APAGE) for gliadins and SDS-electrophoresis for HMW-GS were applied. Electrophoretic analysis revealed that five of the examined local populations, which are registered as durum wheat, are actually bread wheat. The predominant alleles in both the groups of Hellenic durum wheats are *Gli-A1r, Gli-B1h, Glu-A1c, Gli-B2-1.* At the *Glu-B1* locus the allele *Glu-B1b* associated with better quality predominates among the cultivars (58%), whereas the allele *Glu-B1e* (50%) shows the highest frequency among the local populations. Only three samples, two cultivars (Syros and Lemnos) and one local population (Local of Heraklio), carry the gene locus *Gli-B1* component *γ42,* which is an index of inferior end product quality. Higher genetic diversity at the studied storage protein loci of the homoeologous group 1 chromosomes *(Glu-A1, Glu-B1, Gli-A1, Gli-B1)* was recorded in the local Hellenic populations of durum wheat compared to the group of the Hellenic commercial cultivars. The results suggest their potential for widening the gene pool of commercial durum wheat cultivars.

Keywords: durum wheat, allelic diversity, glutenins, gliadins, cultivar, description, purity

Introduction

Durum wheat *Triticum turgidum* ssp. *turgidum* convar. *durum* (Desf.) MacKey is an important crop used primarily for making pasta products, and in some cases for making bread (Sissons 2008). In wheat, the dough properties such as elasticity and extensibility are determined by the composition and ratio of gluten proteins, glutenins and gliadins, the main seed storage proteins (Miflin et al. 1983; Payne 1987). Gliadins are monomeric alcohol-soluble proteins, which can be divided into four groups by acid polyacrylamide gel electrophoresis (APAGE): α-, β-, γ- and ω-gliadins (Woychik et al. 1961). The ω-gliadins

* Corresponding author; E-mail: xynias@teikal.gr

(molecular weight of 44–78 kd) are S-poor prolamins whereas α-, β- and γ-gliadins (molecular weight of 36–44 kd) are S-rich (Miflin et al. 1983). Glutenins are large aggregates of subunits joined by disulphide bonds. Glutenin subunits are divided into two classes: low-molecular-weight glutenin subunits (LMW-GS) (31–51 kd) and high-molecular-weight glutenin subunits (HMW-GS) (80–140 kd) (Payne and Corfield 1979). LMW-GS comprise 60–80% of the glutenin portion (Sissons 2008) and contribute to durum wheat gluten strength (Sissons et al. 2005).

In durum wheat (2n = 4x = 28, AABB), gliadins are encoded by the four major loci *Gli-A1, Gli-B1, Gli-A2, Gli-B2* located at the ends of the short arms of homoeologous group 1 and 6 chromosomes (Joppa et al. 1983). *Gli-A1* and *Gli-B1* loci are closely linked to the loci *Glu-A3,* and *Glu-B3* encoding most of the LMW glutenin subunits (Ruiz and Carrillo 1993). HMW-GS loci *Glu-A1* and *Glu-B1* are located on the long arms of homoeologous group 1 chromosomes (Payne 1987) and code for 0–1, 1–2 subunits, respectively. A minor locus encoding a B subunit of LMW and one–two ω-gliadins, *Gli-B3* (Ruiz and Carrillo 1993), also previously designated *Glu-B2* (Jackson et al. 1985), was identified on a distance of about 20 cM from the *Gli-B1/Glu-B3* loci.

A special feature of wheat storage protein loci is multiple allelism. Among 502 durum wheat cultivars, 7 and 11 alleles were identified at the *Glu-A1* and *Glu-B1* loci, respectively (Branlard et al. 1989). It should be noted that among the durum wheat alleles certain alleles were similar to the respective in bread wheat (such as *a, b* and *c* at *Glu-A1* and *a, b, d, e, f* and *h* at *Glu-B1*), whereas some other were specific "durum" alleles. Nine B-LMW-GS alleles were identified in both of the *Glu-A3* and *Glu-B3* loci (Nieto-Taladriz et al. 1997; Martinez 2004) and this number was further increased, since eight and 11 new alleles were identified at the *Glu-A3* and *Glu-B3* loci, respectively, in Spanish landraces (Aguiriano et al. 2008). The patterns of B-LMW-GS alleles at the *Glu-B3* locus contain more components (4–5) than those at the *Glu-A3* locus (0–3). Even more alleles (gliadin blocks of 1–6 components) were identified at the major gliadin loci, and more precisely, 10 at *Gli-A1* and 12 at *Gli-B1* locus (Kurdyavtsev et al. 1996; Letta et al. 2005; Kudryavtsev 2007).

Due to their high level of polymorphism, storage proteins, including gliadins, can be used as effective genetic markers for diversity analysis of collections of durum wheat varieties and local populations, controlling purity and identity of accessions, especially those preserved in Gene Banks (Aguiriano et al. 2006). Aim of the present study was to evaluate the allelic composition of 12 Hellenic commercial cultivars and 17 local durum wheat populations, kindly provided from the Hellenic Gene Bank, with respect to gliadin and HMW GS loci.

Materials and Methods

Plant material

Ten commercial durum wheat cultivars (Mexicalli E, Athos, Selas, Skiti, Syros, Sifnos, Kallithea, Pontos, Papadakis, Anna), three old durum cultivars (Lemnos, Electra and

Nteves) and seventeen indigenous to Hellas durum populations were analyzed for their seed storage protein composition. The commercial cultivars were developed at the Cereal Institute of Thessaloniki (Anonymous 1991), Hellas, in the last thirty years and most of them are registered in the Hellenic List of Cultivated varieties. The populations were collected from various places all over Hellas by the Hellenic Gene Bank, which is responsible for their collection, description and preservation.

Seed protein electrophoresis

Twenty-five individual seeds from each cultivar were used for electrophoretic analysis to determine the alleles at the storage protein loci *Gli-A1, Gli-B1, Glu-A1, Glu-B1,* as well as *Gli-A2, Gli-B2*. Acid polyacrylamide gel electrophoresis (APAGE) for gliadins (Kozub et al. 2009) and SDS-electrophoresis for HMW-GS (Laemmli 1970) were applied. HMW-GS alleles were determined using the catalogue of Payne and Lawrence (1983). Gliadin alleles were identified according to the catalogue of Metakovsky (1991). For the identification of the gliadin and glutenin subunits, bread wheat cultivar Bezostaya 1 was used as the standard (control). In the case of the *Gli-A1r, Gli-A1m, Gli-B1d* and *Gli-B1h* alleles, the cultivar Rannyaya 73, the *Gli-A1m* near-isogenic line of Bezostaya 1, the cultivars Dneprovskaya 521 and Krasnodonka, respectively, were used as the standards. Alleles designated by two or more symbols with asteriscs are gliadin alleles that are absent in the basic catalogue of Metakovsky (1991). They seem to be inherent to durum wheat and their designations should be revised. Alleles at *Gli-A2, Gli-B2* were designated in this study by numbers for differentiating the cultivars.

Statistical analysis

Genetic similarities between the examined cultivars were determined using the NTSYS pc version 2.1 (Rohlf 2000) statistical program and the corresponding dendrograms were constructed with SM coefficient.

Results

The electrophoretic patterns of HMW-GS and gliadins of the durum wheat germplasm have shown that five of the local populations, registered by the Hellenic Gene Bank as durum, were actually bread wheat (Table 1). One of the commercial cultivars (Kallithea at the *Gli-A1* locus), the old cultivar "Nteves" (at the *Gli-B1* and *Glu-A1* loci), two of the local populations ("Chios red-wheat" at the *Glu-A1* locus, "Chios white-awn" at the *Glu-B1* locus) were found to be polymorphic (Table 1).

The analysis of the genotypes revealed the presence of 7 alleles at the *Gli-A1* and *Gli-B2* loci, 6 alleles at the *Gli-B1* locus, 5 alleles at the *Glu-B1* locus, and finally 3 at the *Glu-A1* and *Gli-A2* loci (Table 2). The predominant alleles in the total group of the Hellenic samples are *Gli-A1r, Gli-B1h, Glu-A1c, Glu-B1e* and *b, Gli-A2-2* and *1* and *Gli-B2-1* (in 72, 71, 92, 42, 33, 58, 37.5 and 46% of the samples, respectively, Table 2). In the commercial cultivars, four alleles at the *Gli-A1* locus, two at *Gli-B1*, three at *Glu-B1* and *Gli-A2* were identified. The highest number of alleles (six) was detected at the *Gli-B2*

Table 1. Genotypes at gliadin and high-molecular-weight glutein subunit loci of Hellenic durum wheat germplasm and frequencies of different biotypes

N	Name	Cultivar type	Note	*Gli-A1*	*Gli-B1*	*Glu-A1*	*Glu-B1*	*Gli-A2*[1]	*Gli-B2*[2]	*Gli-D1*[3]	*Glu-D1*[3]
1	Mexicalli E	Reg. cult.		*r*	*h*	*c*	*b*	1	1		
2	Athos	Reg. cult.		*b*[d]*	*h*	*c*	*e*	2	4		
3	Selas	Reg. cult.		*r*	*h*	*c*	*b*	1	1		
4	Skiti	Reg. cult.		*r*	*h*	*c*	*d*	1	2		
5	Syros	Reg. cult.		*r*	*in**	*c*	*b*	2	3		
6	Sifnos	Reg. cult.		*r*	*h*	*c*	*b*	1	1		
7	Kallithea	Reg. cult.		*r* + *g*	*h*	*c*	*e*	2	4		
8	Pontos	New rel.		*r*	*h*	*c*	*b*	1	1		
9	Papadakis	New rel.		*r*	*h*	*c*	*b*	1	7		
10	Anna	New rel.		*r*	*h*	*c*	*b*	1	1		
11	Aegean black-awn	Population		*r*	*h*	*c*	*e*	2	1		
12	Lemnos	Cult. past		*m*	*in**	*c*	*e*	5	5		
13	Dimini Aetoloakarnanias	Local pop.		*r*	*hn**	*c*	*d*	1	4		
14	Durum Aetoloakarnanias	Local pop.	*T. aestivum*	*d*	*o* + *m* + *h*	*a* + *c*	*a* + *b* + *h*				*a* + *d*
15	Mavratheri	Local pop.		*r*	*h*	*c*	*e*	2	1		
16	Local of Thessalia	Local pop.		*p*	*hn**	*c*	*d*	2	1		
17	Population of Kos	Local pop.		*r*	*h*	*c*	*e*	2	4		
18	Nteves	Cult. past		*r*	*hno** + *d*	*a* + *b*	*e*	2	6		
19	Argolian black-awn	Local pop.	*T. aestivum*	*k*	*c*	*b*	*i*			*b*	*a*
20	Population of Samos	Local pop.		*r*	*h*	*c*	*e*	2	1		
21	Local of Heraklio	Local pop.		*brd**	*in**	*c*	*d*	2	6		
22	Chios white-awn	Local pop.		*r*	*h*	*c*	*d* + *b*	1	2		
23	Chios red-wheat	Local pop.		*rn**	*h1**	*a* + *b*	*h*	2	1		
24	Black-awn of Corfu	Local pop.	*T. aestivum*	*o*	*o*	*a*	*b*			*e*	*d*
25	Ac. No. 4679	Local pop.		*r*	*h*	*c*	*e*	2	1		
26	Ac. No. 1783	Local pop.	*T. aestivum*	*o*	*b*	*a*	*c*			*f*	*a*
27	Electra	Cult. past		*r*	*h*	*c*	*e*	2	4		
28	Population of Lesvos	Population	*T. aestivum*	*m*	*o*	*b*	*e*			f	a
29	Population of Chios	Population		*rn**	*h*	*c*	*f*	2	4		

Note: * new alleles

[1,2] Designations of alleles at *Gli-A2* and *Gli-B2* in this set of samples (not according to any catalogue), similar numbers refer to similar alleles, [3] Bread wheat

locus, but the cultivars did not differ at the *Glu-A1* locus (Table 2). In this group, the predominant alleles were *Gli-A1r* (89%), *Gli-B1h* (83%), *Glu-A1c* (100%), *Glu-B1b* (58%), *Gli-A2-1* (58%) and *Gli-B2-1* (42%). In the local populations, six alleles were detected at the *Gli-B1* locus, five at *Glu-B1,* four at *Gli-B2* and *Gli-A1,* three at *Glu-A1* and two at *Gli-A2*. The predominant alleles in this group were: *Gli-A1r* (67%), *Gli-B1h* (58%), *Glu-A1c* (83%), *Glu-B1e* (50%), *Gli-A1-2* (83%) and *Gli-B2-1* (50%, Table 2).

The examined group of the Hellenic cultivars and populations was classified into two equally major classes, three minor and one single class (Fig. 1). In the first major class, four cultivars ("Mexicalli", "Selas", "Pontos" and "Anna") were found identical, whereas two other cultivars ("Sifnos" and "Papadakis") and one population ("Chios white-awn 1")

Table 2. Frequencies of gliadin and high-molecular-weight glutein subunit alleles in Hellenic durum wheat cultivars and local populations

Locus	Allele	Frequency		
		Total sample	Cultivars	Local populations
Gli-A1	*r*	**0.729**	**0.792**	**0.667**
	*rn**	0.083		0.167
	m	0.042	0.083	
	p	0.042		0.083
	*bd**	0.042	0.083	
	*brd**	0.042		0.083
	g	0.021	0.042	
Gli-B1	*h*	**0.708**	**0.833**	**0.583**
	*in**	0.125	0.167	0.083
	*hn**	0.083		0.167
	*h1**	0.042		0.083
	*hno**	0.021		0.042
	d	0.021		0.042
Glu-A1	*c*	**0.917**	**1.000**	**0.833**
	a	0.042		0.083
	b	0.042		0.083
Glu-B1	*e*	**0.417**	0.333	**0.500**
	b	0.333	**0.583**	0.042
	d	0.188	0.083	0.292
	h	0.042		0.083
	f	0.042		0.083
Gli-A2	2	**0.583**	0.333	0.833
	1	0.375	**0.583**	0.167
	5	0.042	0.083	
Gli-B2	1	**0.458**	**0.417**	**0.500**
	4	0.250	0.250	0.250
	2	0.083	0.083	0.083
	6	0.083		0.167
	3	0.042	0.083	
	5	0.042	0.083	
	7	0.042	0.083	

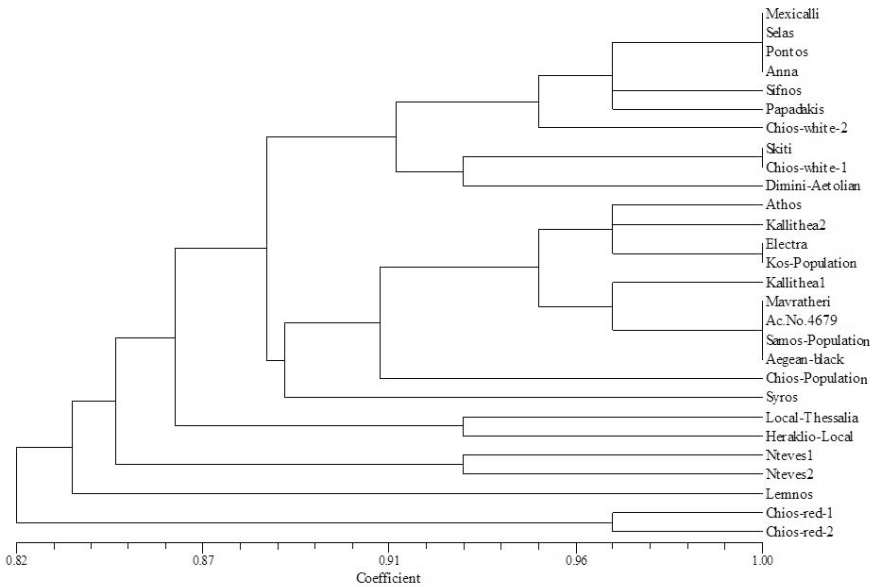

Figure 1. Dendrogram of existing similarities among and within the examined Hellenic durum cultivars and populations based on genotypes at gliadin and HMW-GS loci

were found closely related. The second allele combination within the "white-awn population of Chios" ("Chios white-awn 2") was identical to cultivar "Skiti". A similar view could be observed in the second major class. Cultivar "Syros", although belonging to the second major class, was less related to the other members of the class. Six of the local populations were equally distributed to the three minor classes (two populations per class). Finally, cultivar "Lemnos" was found to be less related to all other Hellenic cultivars and populations.

Discussion

Storage proteins have been used for a long time in studying the genetic variability of bread and durum wheat cultivars and landraces from different countries (Branlard et al. 1989; Kurdyavtsev et al. 1996; Igrejas et al. 1999; Letta et al. 2005; Aguiriano et al. 2006, etc.). The present study was focused on the existing variation at the gliadin and HMW-GS loci, in Hellenic durum wheat germplasm, which was never examined in the past. Storage proteins (gliadins and HMW-GS) are a valuable tool for the registration of accessions, assessment of their identity and purity, and this was demonstrated by the identification of five bread wheat populations which were previously registered as durum (Table 1). The last could be explained by the fact that registration was probably based mainly on morphological traits, supporting the view that more accurate tests must be employed in cultivar identi-

fication and description (Cooke 1995). Thus, the use of biochemical markers, which are not affected by the environment, is strongly recommended.

Comparisons of allele frequencies in the samples of cultivars and local populations revealed that the predominant alleles at four loci were analogous in either groups *(Gli-A1r, Gli-B1h, Glu-A1c, Gli-B2-1)*. Differences in the predominant alleles were observed only at the *Glu-B1* and *Gli-A2* loci. The alleles *Glu-B1b* and *Gli-A2-1* were the most common among the durum wheat cultivars, whereas the alleles *Glu-B1e* and *Gli-A2-2* were the most frequent among the local populations (Table 2). Both groups differed in the number and constitution of storage protein alleles confirming previous reports (Sissons 2008). At the *Gli-A1* locus, although either group of samples had four alleles, three of them (alleles *m, g* and b^d*) were only identified in the cultivars and other three (alleles *rn*, p* and br^d*) were only found in the group of the local populations. At the *Gli-B1* locus, the commercial cultivars were less polymorphic: two alleles were detected in their group compared to six alleles that were observed in the local population group. It should be noted that the predominant alleles at the gliadin loci *Gli-A1* and *Gli-B1* as well as at the HMW-GS loci *Glu-A1* and *Glu-B1* in both the groups were similar to those identified in bread wheat, according to the catalogues of Payne and Lawrence (1983) and Metakovsky (1991). The predominant allele *Gli-B1h* and the rare allele *h1** which was observed only in "Chios redwheat" have the component γ-45 like in the alleles *b* and *c* according to the designations presented in the catalogue of Kudryavtsev (2007). The rare alleles *Gli-B1hn** and *hno** have a component similar to γ-44. Such a case has also been reported in Spanish durum wheats in the alleles *Gli-B1new-1* and *new-3* (Aguiriano et al. 2006) and in the alleles *e* and *l* (Kudryavtsev 2007). The allele *Gli-B1in*,* with the component γ-42, similar in the allele *a* according to Kudryavtsev (2007) was detected in only three accessions: two cultivars ("Syros" and "Lemnos") and one population ("Local of Heraklio", Table 1). It was demonstrated that γ-gladins encoded by genes at the *Gli-B1* locus could serve as genetic markers for gluten quality (Damideaux et al. 1978) mostly due to their linkage to LMW-GS encoded by genes at the *Glu-B3* locus (Skerritt 1998). Later studies have shown that virtually always the presence of the gliadin γ-42 component was associated with the LMW GS alleles *Glu-B3b* and *i* and is related with poor pasta quality (Payne et al. 1984; Carrillo et al. 2000). On the other hand, forms containing the gliadin γ-45 component exhibited good quality when linked with the alleles *Glu-B3a* and *c,* intermediate when linked with the LMW GS alleles *d, f, g* and *h*, and poor quality, in combination with the allele *Glu-B3e* (Carrillo et al. 2000). However, Sissons et al. (2005) reported that the allele *Glu-B3f* was also associated with poor quality. The gliadin allele component γ42, which is mostly associated with low gluten strength, was detected in three accessions (12.5% of the total Hellenic durum accessions analyzed) – in the commercial cultivar "Syros", in the old cultivar "Lemnos" and in the local "population of Heraklio" (8.3% of local populations, Table 2). The proportion of landraces possessing the γ-42 component [allele $Gli\text{-}B1^d a$ according to Kudryavtsev (2007)] that was detected among a sample of Spanish durum wheat landraces was 16.6% (Aguiriano et al. 2006). The frequency of the alleles with γ-42 that was revealed among the Hellenic durum wheat germplasm is comparable to the aver-

age frequency of the allele *Glu-B3b* associated with γ-42 that was detected in durum wheat landraces from the South East Europe (14.29%, Moragues et al. 2006).

At the *Glu-A1* locus the Hellenic durum cultivars were monomorphic (only the allele *c* was recorded), whereas three alleles were detected in the local populations. The predominance of the allele *Glu-A1c* (the null allele) was also detected in collections of durum wheat from different countries, for example in Portuguese cultivars (Igrejas et al. 1999), in French cultivars (Branlard et al. 1989), in Canadian and Australian wheats (Sissons et al. 2005), and in the ICARDA wheat collection (Raciti et al. 2003). The frequency of this allele in the Hellenic local populations was 83.3% and a similar frequency (78.6%) was also detected in the South East Europe region (Moragues et al. 2006). Thus, as indicated by its worldwide predominance among durum wheats, the allele *Glu-A1c* seems to be beneficial to pasta quality. The last is not correlated with gluten strength. According to SDS sedimentation volume, an index of gluten strength, this allele ranks last *(a = b > c)* (Martinez et al. 2004).

At the *Glu-B1* locus, the Hellenic cultivars were also less polymorphic (three alleles were found) compared to the local populations, where six alleles were identified (Table 2). This lack of variability at the above loci was also observed in current Italian cultivars (Beretta 1989, referred by Raciti et al. 2003) and for this Raciti et al. (2003) suggested the need of incorporating more alleles at these loci to improve quality. The frequency of the predominant allele *Glu-B1b* in the Hellenic cultivars was high (58%), whereas lower frequencies were reported in French cultivars (15.8%, Branlard et al. 1989), in Portuguese cultivars (36.4%, Igrejas et al. 1999), and in Canadian (15%, Sissons et al. 2005). This high frequency of the *Glu-B1b* allele was also observed in Australian durum wheats (69%, Sissons et al. 2005). In contrast, in the Hellenic local populations, the allele *(Glu-B1e)* was the most frequent one (50%). This value is much higher than the one observed in landraces from South East Europe (7.14%) and from the total value of the Mediterranean basin (23.81%, Moragues et al. 2006). However, this is close to the frequency of the *e* allele observed in the ICARDA collection (44.82%, Raciti et al. 2003). An association of GS to gluten strength in durum wheat was revealed and it was demonstrated that HMW-GS 20 (the *Glu-B1e* allele) affects negatively the quality and that the alleles *Glu-B1b* or *Glu-B1d* have a positive effect. For this, breeders were recommended to avoid parents with the *Glu-B1e* allele (Pena et al. 1994; Brites and Carrillo 2001; Sissons et al. 2005). At least half of the local Hellenic populations cannot be used as sources of high-quality alleles at the *Glu-B1* locus. However, they might be useful as sources of resistance to biotic or abiotic stresses and in crosses where these forms should involve another parent with *Glu-B1* allele of "good quality" but this has to be further investigated. In addition, their allele composition at *Glu-3* loci should be studied, as LMW GS are more important contributors to gluten strength than HMW GS (Sissons et al. 2005).

It was demonstrated in the present study that most modern Hellenic cultivars, including the newly-released ones, carry the allele combination *Gli-A1r, Gli-B1h, Glu-A1c, Glu-B1b, Gli-A2-1*. This combination is most likely due to the association of these alleles with grain quality (Sissons 2008). A similar predominant association is observed also in the Hellenic local populations at three marker loci: *Gli-A1r, Gli-B1h, Glu-A1c.* Besides

the association with grain quality, the presence of similar predominant alleles at the storage protein loci both in cultivars and local populations may indicate their adaptive value: the presence of these marker alleles may be associated with tolerance to stress factors during vegetation. At least partial adaptive value of protein polymorphism was demonstrated in emmer wheat by Nevo et al. (2002). Correlation of the genetic variation and the allele frequencies at HMW glutenin subunit loci in wild emmer wheat and their associations to the climatic and natural factors were also revealed (Nevo and Payne 1987; Levy and Feldman 1988).

Most of current Hellenic cultivars were found to be more or less identical at the loci studied (Fig. 1). This elucidates the narrowing of the genetic background of the crop (especially at certain loci), suggesting that more variability must be incorporated in modern breeding programs. A part of this variability could be mined in the local populations, which form the second major group of the present study. The local "population of Thessalia" (Central Hellas) was more related to the respective "population of Heraklio" (Krete island), probably indicating some common dietary practices of local populations. The old cultivar "Lemnos" was found to be less related to all other Hellenic cultivars and populations (Fig. 1). This cultivar, as was previously referred, carries the gene locus *Gli-B1* component γ-42, which is associated with inferior quality (Damideaux et al. 1978), and this was verified by all relevant quality tests (Cereal Institute of Thessaloniki, unpublished data). Cultivar "Lemnos" is a tall cultivar, susceptible to lodging. However, due to its cold resistance, especially in spring, and its early heading emergence (Anonymous 1978) it is quite a popular germplasm. Therefore, it is suggested to be used only in specific breeding projects taking into account its disadvantages.

The higher allelic diversity at the studied storage protein loci of the homoeologous group 1 chromosomes *(Glu-A1, Glu-B1, Gli-A1, Gli-B1),* which are more strongly associated with quality as compared with *Gli-2* loci (Skerritt 1998), recorded in the Hellenic local populations of durum wheat indicates the potential for their use in breeding programs as sources of new storage protein alleles for widening the gene pool of commercial cultivars.

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